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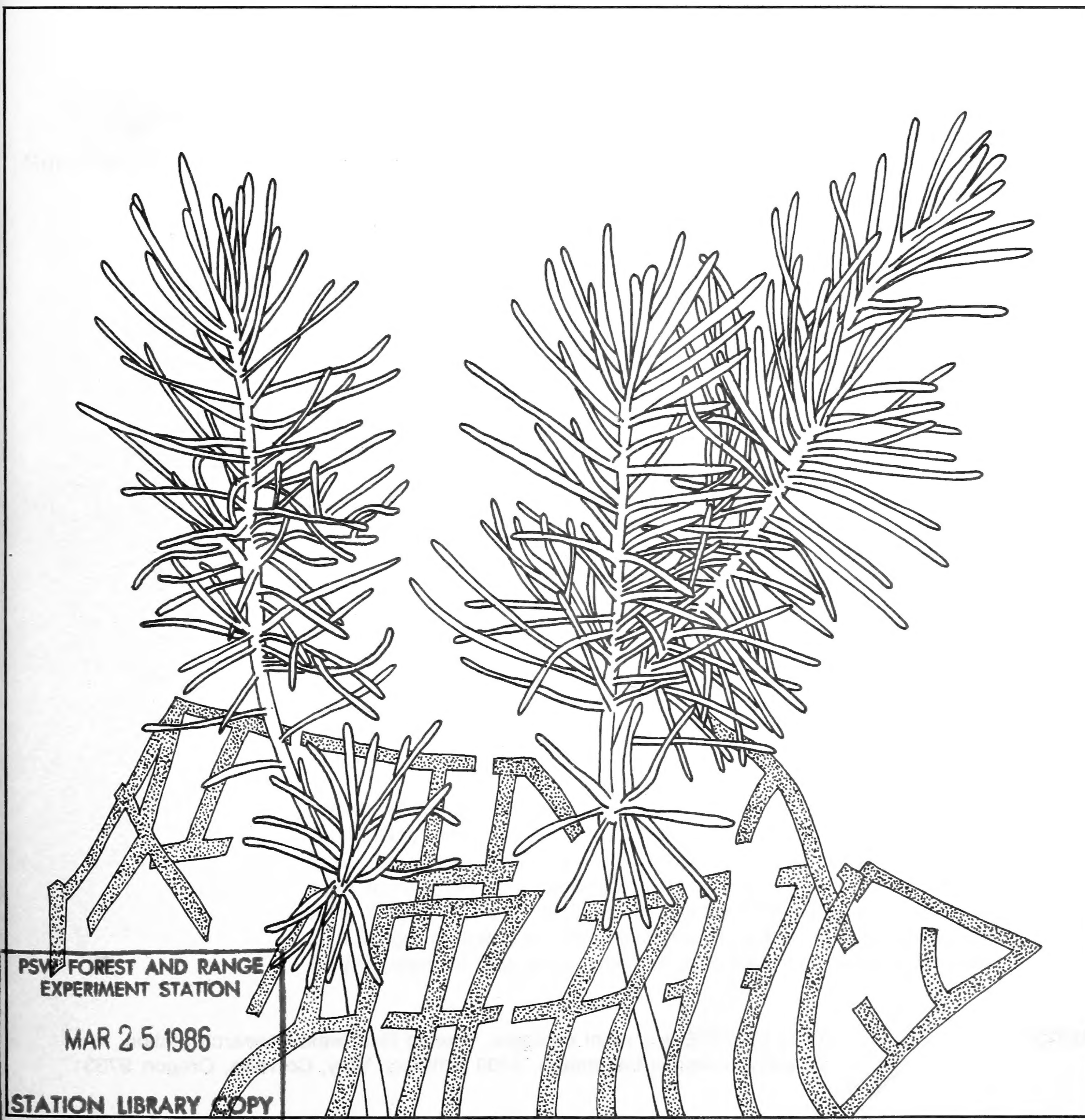
Germination, Survival and Early Growth of Conifer Seedlings in Two Habitat Types

Don Minore



Author

DON MINORE is a plant ecologist, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331.

Abstract

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Conifer seeds were sown in clearcut *Abies amabilis/Achlys triphylla* and *Abies amabilis/Vaccinium membranaceum/Xerophyllum tenax* habitat types in the McKenzie River basin in Oregon to determine ratios of seeds to established seedlings. Protection from animal predation and shade from stumps were beneficial, but survival and growth did not differ significantly between habitat types or among humus treatments. Germination in the greenhouse was earlier and more prolonged on soils from the *Achlys* type.

Keywords: Seedling growth, habitat types, seedling survival, germination (seed).

Summary

Many conifer seeds are dispersed from mature conifer stands, but most do not survive to become established seedlings. I investigated seed and seedling mortality in two field tests and a greenhouse experiment.

Douglas-fir, western hemlock, Pacific silver fir, and noble fir seedlings failed to survive their first growing season when seeds were sown on a few large, consolidated seedbeds in clearcuts in the McKenzie River basin in Oregon. Severe seed predation and high surface soil temperatures occurred on these exposed seedbeds in both the *Abies amabilis/Achlys triphylla* and *Abies amabilis/Vaccinium membranaceum/Xerophyllum tenax* habitat types. No significant differences in seedling survival between habitat types were measured, but summer surface soil temperatures were higher on clearcuts in the *Achlys* type.

Douglas-fir seeds survived much better when sown in small, scattered seed spots on the same clearcuts. Habitat type and the addition of mycorrhizal inoculum (forest humus) did not significantly affect first- and second-year survival or growth of seedlings in this second field test. Seed spots shaded by stumps had better survival and growth than seed spots located on open microsites, however; and the protection from animal predation afforded by staked-down plastic berry baskets was very beneficial. For a Douglas-fir seed lot capable of 100-percent germination, about 75 seeds would be required to establish one 2-year-old seedling on clearcut, unprotected mineral soil seedbeds in the *Achlys* and *Xerophyllum* habitat types where those seedbeds are shaded by stumps. About 190 seeds would be required where the seedbeds occur on open, unshaded microsites.

Results of the greenhouse experiment suggest that an unmeasured factor like soil microbiology may significantly influence conifer seed germination in the two habitat types. Soils from the *Achlys* and *Xerophyllum* types were found to be similar in color, texture, pH, and nutrient content; but Douglas-fir, western hemlock, Pacific silver fir, and noble fir seeds began germinating earlier and continued to germinate for a longer period in an unheated greenhouse when sown on soils from the *Achlys* clearcuts than when sown on soils from the *Xerophyllum* clearcuts.

Contents

Introduction

Seed germination and seedling survival in the field are as important to natural forest regeneration as are the production and dispersal of seeds. Many seeds are produced and dispersed, but most do not germinate or they fail to survive after germination. This severe seed and seedling mortality multiplies the number of seeds required to obtain natural regeneration. It also acts as a selective factor in determining the genetics of future stands.

The relation of dispersed seed populations to established seedling populations is not well known for most high elevation forests in the Pacific Northwest. Production and dispersal of conifer seeds in the *Abies amabilis* forest zone described by Franklin and Dyrness (1973) have been well studied (Carkin and others 1978; Franklin and others 1974; Franklin and Smith 1974a, 1974b), but little work has been done on the fate of those seeds. Sullivan (1978) compared forest regeneration on clearcuts in several habitat types within the *Abies amabilis* zone and concluded that regeneration differed significantly among habitat types, but he did not relate his observations and conclusions to the seed supply. Neither did Halverson and Emmingham (1982), who were unable to correlate forest regeneration in the *Abies amabilis* zone with habitat types, but found extremes in environment to be the most probable cause of regeneration failure. Seidel (1979a) surveyed mixed conifer regeneration on many clearcuts along the east side of the Cascade Range and in the Blue Mountains of Oregon. He measured the variation among plant community types and geographic locations, but did not relate established regeneration to amounts of seed or early seedling mortality and did not derive any ratios for seeds to established seedlings. Seidel (1979b) also studied regeneration after shelterwood cutting in a grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.)-Shasta red fir (*Abies magnifica* var. *shastensis* Lemm.) stand in central Oregon. The number of sound seeds collected in his seed traps can be compared to the number of seedlings that became established during the 5-year measurement period to derive seed-to-seedling ratios for four slash treatments under three overstory densities. Those ratios varied from about 25:1 on bulldozed seedbeds under an overstory with basal area of 20.7 square meters per hectare to about 105:1 on undisturbed seedbeds under the same overstory.

Frenzen and Franklin (in press) sowed seeds of noble fir (*Abies procera* Rehd.), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), lodgepole pine (*Pinus contorta* Dougl. ex Loud), and western white pine (*Pinus monticola* Dougl. ex D. Don) on freshly deposited Mount St. Helens tephra. They covered the seeds with wire screen cones, but lost 90 percent through a combination of surface erosion and rodent predation. Failure by seeds to penetrate the tephra surface crust as well as high surface temperatures killed many of the remaining seeds. After 2 years, seed-to-established seedling ratios on these screened tephra seedbeds ranged from 11:1 (Douglas-fir) to 333:1 (western hemlock).

Information on seed and seedling populations at lower elevations in the Pacific Northwest is scarce. Gashwiler (1967, 1970) studied the survival in clearcuts of Douglas-fir, western hemlock, and western redcedar (*Thuja plicata* Donn ex D. Don) seeds from dispersal through the end of germination. Gashwiler did not record postgermination mortality, and he did not measure variation among clearcut locations or habitat types. Radio tagging with Scandium^{46} was used by Lawrence and Rediske (1962) and Black (1969) to determine the fate of Douglas-fir seeds

during the first year after sowing. The scandium treatment interfered with germination, however, and habitat types were not considered in these radio-tagging studies.

The most comprehensive evaluation of seed fate in the Pacific Northwest was done by Zobel (1980). He sowed Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) seeds on four seedbed types in each of four southwestern Oregon plant communities. Zobel used local seed sources, set out known amounts of seed during the autumn seedfall season, and tallied germination, seedling survival, and seedling heights for 3 years. His results are applicable to low-light (1 percent to 8 percent full sun), understory conditions.

Information on seed fate and seedling survival is available for several seeding experiments in the Rocky Mountain region. Burned, clearcut conditions were used by Loewenstein and Pitkin (1966) in studying the effects of sowing season and seedbed cultivation on the emergence and first-year survival of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), Douglas-fir, grand fir, and western redcedar seeds sown at unspecified depths on a 0.1-hectare area in northern Idaho. Survival of their seedlings ranged from less than 1 percent to about 17 percent. Radvanyi (1966) determined the influence of small mammals on the direct seeding of white spruce (*Picea glauca* Moench) Voss) on two clearcut areas near Hinton, Alberta. His spruce seeds were treated with endrin and coated with aluminum powder, but half were destroyed during the summer. Lotan and Perry (1977) treated lodgepole pine seeds with endrin and anthraquinone before sowing them on nine seedbed treatments in three habitat types in southwestern Montana and southeastern Idaho. They recorded seed-to-seedling ratios that were inversely related to moistness of the habitat. The results of all three of these experiments are most applicable to artificial regeneration by direct seeding.

Direct seeding was used by Alexander (1983, 1984) to relate environmental factors to the germination and survival of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings after clearcutting in the Rocky Mountains of Colorado. He found drought to be the most serious cause of mortality and obtained his best seed-to-seedling ratio (32:1) by using scarified, shaded seedbeds on a north aspect. Rodents were excluded from those seedbeds, however; and rodent predation is one of the most important factors influencing natural regeneration. Rodents were not excluded from the clearcut openings in which Alexander (1969) studied the natural seedfall and establishment of Engelmann spruce, but most surviving seedlings were confined to scarified seedbeds at the margins of those clearcuts.

Natural regeneration on clearcuts was also studied by Noble and Ronco (1978). They measured the seed production and seed dispersal of Engelmann spruce and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) for 10 years and monitored seedling establishment and survival for 14 years to determine the ratios of seeds to established seedlings for five National Forests in Colorado. The ratios varied with clearcut size, seedbed, and other environmental conditions. They ranged from 167:1 to indeterminant (no surviving seedlings).

Seed-to-seedling ratios are needed for Pacific Northwest forests. It is difficult to judge the adequacy of seed dispersal or compare artificial and natural regeneration without relating the number of seeds dispersed to the number of naturally established seedlings that result. Perry and others (1982) show that the growth of those established seedlings may be reduced by changes in soil mycorrhizae that are associated with clearcutting, and Harvey and others (1979) found differences in the distribution of ectomycorrhizae among habitat types. Parke and others (1983) found that forest litter and humus include mycorrhizal inoculum.

Artificial regeneration is difficult, and natural regeneration is slow and erratic in several habitat types within the *Abies amabilis* forest zone. I measured seed germination, seedling survival, and early seedling growth on two of those difficult-to-regenerate habitat types in the McKenzie River basin, then calculated seed-to-established seedling ratios. This study had five objectives:

1. To compare seedling establishment and early growth in the *Abies amabilis/Achlys triphylla* and *Abies amabilis/Vaccinium membranaceum/Xerophyllum tenax* habitat types.

2. To compare the effect of soil on seed germination and early seedling growth in the two habitat types.

3. To estimate the effect of animal predation on seedling establishment.

4. To compare the effect of two microenvironments on seedling survival.

5. To determine the effect of adding mycorrhizal inoculum (forest humus) to mineral soil seedbeds in clearcuts.

Methods

Table 1—Locations and physiography of the clearcuts

Clearcut	Location 1/	Elevation	Aspect azimuth	Slope
		Meters	Degrees	Percent
Achlys 1	SW1/4NE1/4S8T14SR6E	1 220	200	20
Achlys 2	NE1/4NW1/4S19T14SR6E	1 310	135	45
Achlys 3	NW1/4NE1/4S29T15SR6E	1 370	180	40
Achlys 4	SE1/4SE1/4S18T15SR6E	1 340	225	65
Xerophyllum 1	SE1/4NW1/4S34T14SR6E	1 400	248	15
Xerophyllum 2	SW1/4NE1/4S28T14SR6E	1 490	105	40
Xerophyllum 3	NE1/4SW1/4S33T15SR6E	1 520	260	60
Xerophyllum 4	NW1/4SW1/4S5T16SR6E	1 340	40	30

1/ From the Willamette Meridian.

I selected eight clearcuts in the McKenzie River basin that were most representative of the habitat types to be studied. Four clearcuts were in the *Abies amabilis/Achlys triphylla* habitat type, and four were in the *Abies amabilis/Vaccinium membranaceum/Xerophyllum tenax* type. Two clearcuts in each habitat type were located in the H.J. Andrews Experimental Forest; the other two were north of that research facility. All were in the Willamette National Forest, and all were more than 5 years old. Elevations ranged from 1 219 to 1 524 meters. Slopes and aspects varied, but topographic differences were well distributed among habitat types (table 1). A uniform area characteristic of the habitat type was delineated within each clearcut.[1/] I then installed a consolidated-seedbed experiment and collected soil samples for a greenhouse experiment. One year later, a second dispersed-seedbed experiment was installed on the same clearcut areas.

[1/] William H. Emmingham assisted in clearcut selection and delineated the habitat types.

Consolidated-Seedbed Experiment

Four seedbeds were randomly located in each clearcut; sites that fell on stumps, boulders, or other nonsoil material were rejected. Each seedbed was a 3-meter by 2-meter area cleared of all vegetation, humus, roots, and rocks. A 2-meter by 1-meter rectangular subplot was established at the center of each of these four cleared seedbeds. Each subplot was divided into eight 50-centimeter by 50-centimeter squares. Four conifer species were then randomly assigned to those eight squares.

Four of the squares were sown with 250 uniformly distributed seeds of the same species. The seeds received no predation protection. Douglas-fir, western hemlock, Pacific silver fir, and noble fir from the McKenzie River basin were used. Seeds were placed in 1-centimeter depressions but were not covered with soil.[2/]

The other four squares in each subplot were sown with only 50 seeds of the same species. These seeds were sown near the center of the square, in five grid areas, with 10 seeds per area. The seeds on each 10-centimeter by 10-centimeter grid area were then covered with pint-sized berry baskets as recommended by Zechentmayer (1971). The berry baskets were staked down to prevent seed predation by small mammals and birds. Like the unprotected seeds, the seeds protected by berry baskets were placed in depressions but were not covered with soil.

Each of the eight clearcuts (four in each habitat type) contained four 2-meter by 1-meter subplots. Each subplot in a clearcut contained 1,000 unprotected seeds (250 of each species) and 200 protected seeds (50 of each species). Thus, each of the eight clearcuts contained 1,200 seeds of each species, sown at a density of 1,000 seeds per square meter. All those seeds were sown from September 22 through October 2, 1980, when natural seedfall was occurring in the adjacent stands. A few true fir seeds of natural origin probably reached the consolidated-seedbed subplots from those adjacent stands, but they did not affect the Douglas-fir seedling counts.

Immediately after the snow melted in 1981, during the first week of June, maximum-minimum thermometers were installed at the soil surface and at a depth of 5 centimeters on three randomly chosen subplots in each clearcut. All subplots were then visited at 2-week intervals until August and at monthly intervals from August through the middle of October. Seedlings were counted, photographed, and mapped at each visit to determine seed germination and seedling mortality. The thermometers were calibrated at each visit. Maximum and minimum temperatures were recorded for each period between visits.

[2/] Uniform seed distribution was obtained by evenly sowing 10 seeds in each of 25 grid areas in the 50-centimeter square. Each grid area was 10 centimeters by 10 centimeters.

Clearcuts were the replications in this experiment, and seedling numbers on the four subplots were combined for each clearcut. The resulting survival percentages were transformed to arc sines; split plot analyses of variance were used to examine the differences associated with habitat types, species, and predation protection.

Dispersed-Seedbed Experiment

This experiment was established in late October 1981. Twenty stumps were selected in each of the eight clearcut areas used in the consolidated-seedbed experiment. Each stump was at least 30 centimeters in diameter with vertical or nearly vertical sides on the north and east. Vegetation, humus, rotten wood, roots, and rocks were removed to expose mineral soil in a 50-centimeter by 50-centimeter seedbed on the northeast side of each stump selected. A similar 50-centimeter by 50-centimeter mineral soil seedbed was created in an open, unshaded microsite near each of the selected stumps. Thus, 20 seedbed pairs were established in each clearcut. One seedbed in each pair was shaded by a stump. The other seedbed was unshaded. Half of the 20 seedbed pairs were randomly selected for the addition of mycorrhizal inoculum (forest humus). Humus was collected from the humus-mineral soil interface in a stand adjacent to the experimental area--in the same habitat type. A 200-cubic-centimeter portion of this humus was then mixed with the surface soil in a 10-centimeter by 30-centimeter area on each selected seedbed.

Two seed spots were established 10 centimeters apart on each of the 40 seedbeds in each clearcut. Each seed spot was 10 centimeters square. A 10-centimeter-square template with 10 evenly spaced 0.6-centimeter-diameter bolts protruding 1 centimeter from its lower side was pressed against the seedbed surface to create the depressions in which 10 Douglas-fir seeds were placed on each seed spot. The seeds were not covered with soil, but one seed spot on each seedbed was protected from predation by installing a staked-down plastic berry basket. A flip of the coin determined the seed spot to be protected at each seedbed.

One *Achlys* clearcut and one *Xerophyllum* clearcut were randomly selected for temperature measurements. Maximum-minimum thermometers were installed at six randomly selected seedbed pairs in each of these clearcuts. Maximum and minimum soil surface temperatures were then determined at the stump-shaded microsite and the open, unshaded microsite in each selected pair for a single period beginning on July 8 and ending on October 12, 1982.

The numbers and heights of surviving seedlings were recorded in October 1982 and September 1983. Transformed survival percentages and average heights of the 1- and 2-year-old seedlings were subjected to split-split-split plot analyses of variance; the splits were for habitat type, humus addition, microsite, and protection from predation.

Greenhouse Experiment

About 5 000 cubic centimeters of soil were removed from the top 25 centimeters of the seedbed at each of the four consolidated-seedbed subplots in each of the eight clearcuts on September 25, 1980. The four subplot soil collections from each clearcut were combined, homogenized in a concrete mixer, and used to fill four fiber pots.[3/] The 32 soil-filled pots (four from each clearcut) were placed outdoors in a lath house at Corvallis, Oregon, on September 26, 1980. Samples of the potting soil from each clearcut were air dried and analyzed to determine their physical and chemical properties.

I moved the soil-filled pots to an unheated Corvallis greenhouse on January 6, 1981. Each of the four pots from each clearcut was then sown by scattering 50 seeds of the same species on the soil surface.[4/] The seeded pots were arranged in completely random array on a bench in the unheated greenhouse. No supplemental lighting was used.

I examined the pots and counted seedlings every other day for 74 days after sowing. Seedling counts were then continued at weekly intervals for another 131 days. The techniques described by Campbell and Sorensen (1979) were used to calculate days to peak germination, mean germination rate, and the standard deviation of mean germination rate. They were also used to fit germination frequency curves.

Seedlings were thinned to the three largest in each pot on August 13, 1981. No nutrients were added, but the seedlings were watered regularly and kept in the unheated greenhouse until February 1983. The 2-year-old seedlings were then measured to determine shoot height and were washed free of soil, oven-dried, and weighed. Average heights, weights, germination percentages, and days to peak germination were evaluated by factorial analyses of variance. Mean germination rates and their standard deviations were used in multivariate analyses of variance.

[3/] The pots were 21 centimeters in diameter and 24 centimeters deep.

[4/] Seeds came from the same Douglas-fir, western hemlock, Pacific silver fir, and noble fir seed lots used in the consolidated-seedbed experiment. All the seeds were dry and unstratified, but the potted soils remained moist from the day they were collected until this experiment was concluded.

Results

Consolidated-Seedbed Experiment

Most of the seeds sown in the autumn failed to survive until spring. Less than 2 percent of all the unprotected seeds and only 13.9 percent of all the protected seeds survived until the snow melted in May (table 2). Spring survival at the highest elevations was better than survival at the lowest elevations, but surviving seedlings at all elevations died on these exposed, consolidated seedbeds throughout the hot, dry summer of 1981. Average August temperatures were 1.8 °C above normal, and August precipitation was 2.7 centimeters below normal in the northern Oregon Cascades (National Oceanic and Atmospheric Administration 1981). By October all the unprotected seedlings were dead on seedbeds in the *Achlys* habitat type, and only 0.06 percent of the unprotected seedlings survived in the *Xerophyllum* type. October survival was slightly better under the predation protection afforded by staked-down berry baskets, but it averaged only 3.56 percent in the *Xerophyllum* habitat type and 1.38 percent in the *Achlys* type. Variation among clearcuts was extreme, and the observed differences between habitat-type means were not statistically significant.

Table 2—Survival in 1981 of seedlings from seeds sown in September 1980 on exposed mineral soil in consolidated seedbeds, by habitat type, species, predation protection, and date 1/

	Unprotected 2/					Protected 3/						
Habitat type and species	May 20	June 17	July 15	Aug. 4	Sept. 1	Oct. 15	May 20	June 17	July 15	Aug. 4	Sept. 1	Oct. 15
	Percent											
Xerophyllum:												
Douglas-fir	0.75	0.75	0.52	0.40	0.32	0.12	18.50	18.25	15.62	14.38	11.75	8.62
Noble fir	5.25	2.98	2.38	1.22	.60	.08	22.62	17.62	15.38	13.12	7.88	4.75
Pacific silver fir	1.18	.88	.55	.38	.20	.02	10.12	7.50	5.12	4.50	2.12	.75
Western hemlock	1.30	1.30	.75	.58	0	0	9.62	9.50	5.75	3.25	.38	.12
Average, all species	2.12	1.48	1.05	.64	.28	.06	15.22	13.22	10.47	8.81	5.53	3.56
Achlys:												
Douglas-fir	.90	.75	.35	.28	0	0	22.00	21.75	18.12	16.50	8.12	5.12
Noble fir	.28	.18	.08	.02	0	0	12.38	11.25	9.50	5.88	.38	.38
Pacific silver fir	.08	.05	.02	0	0	0	3.88	3.75	2.50	.88	0	0
Western hemlock	1.55	1.48	.55	.10	0	0	12.12	11.00	4.88	.75	0	0
Average, all species	.70	.61	.25	.10	0	0	12.59	11.94	8.75	6.00	2.12	1.38
Both types:												
Douglas-fir	.82	.75	.44	.34	.16	.06	20.25	20.00	16.87	15.44	9.94	6.87
Noble fir	2.76	1.58	1.22	.62	.30	.04	17.50	14.44	12.44	9.50	4.13	2.56
Pacific silver fir	.62	.46	.29	.19	.10	.01	7.00	5.62	3.81	2.69	1.06	.38
Western hemlock	1.42	1.39	.65	.34	0	0	10.87	10.25	5.32	2.00	.19	.06
Average, all species	1.41	1.04	.65	.37	.14	.03	13.91	12.58	9.61	7.41	3.83	2.47

1/ Differences among species, differences between protected and unprotected seedbeds, and the species X protection interaction were all statistically significant (P<0.01).

2/ 4,000 unprotected seeds of each species were sown in each habitat type, in 4 2-meter by 1-meter seedbeds on each of 4 clearcuts. Each seedbed contained 1,000 unprotected seeds (250 of each species) and 200 protected seeds (50 of each species) in randomized blocks.

3/ 800 seeds of each species were sown in each habitat type, on the same seedbeds used for the unprotected seeds. They were protected by covering with staked-down, plastic berry baskets.

The survival differences among species means and between the means of protected and unprotected seedbeds were statistically significant ($P < 0.01$), as was the interaction between species and protection—predation protection benefited Douglas-fir more than it benefited the other species. Douglas-fir appeared to be the most successful species. Less than 10 percent survival really does not constitute success, however, and it might be preferable to say that Douglas-fir failed less severely than did the other species.

Summer maximum temperatures were significantly higher in the *Achlys* habitat type than they were in the *Xerophyllum* type (table 3). Average maximum soil surface temperatures in both habitat types rose to above 40 °C by the end of June

Table 3—Average summer temperature extremes at the seedbeds, by year, habitat type, depth in soil, and microsite

Year, habitat type, and depth in soil	Microsite			
	Open		Stump-shaded	
	Maximum	Minimum	Maximum	Minimum
	°C			
1981: 1/				
Xerophyllum--				
Soil surface	55.9	-4.2		
5-cm depth	37.2	1.1		
Achlys--				
Soil surface	60.6	-2.0		
5-cm depth	41.8	1.6		
1982: 2/				
Xerophyllum--				
Soil surface	51.8	-2.7	50.8	-2.1
Achlys--				
Soil surface	59.3	-.3	57.6	-.2

1/ Each value is the average of 4 clearcuts, from 3 randomly distributed, unshaded maximum-minimum thermometers in each clearcut. The maximum temperatures differ significantly ($P<0.05$) between habitat types.

2/ Temperatures were measured on 1 randomly chosen clearcut in each habitat type during 1982. Each Achlys value is the average of 6 maximum-minimum thermometers located at randomly chosen microsite pairs. Each Xerophyllum value is the average of 4 maximum-minimum thermometers (thermometers were destroyed at 2 microsites). These single-clearcut measurements were not analyzed statistically.

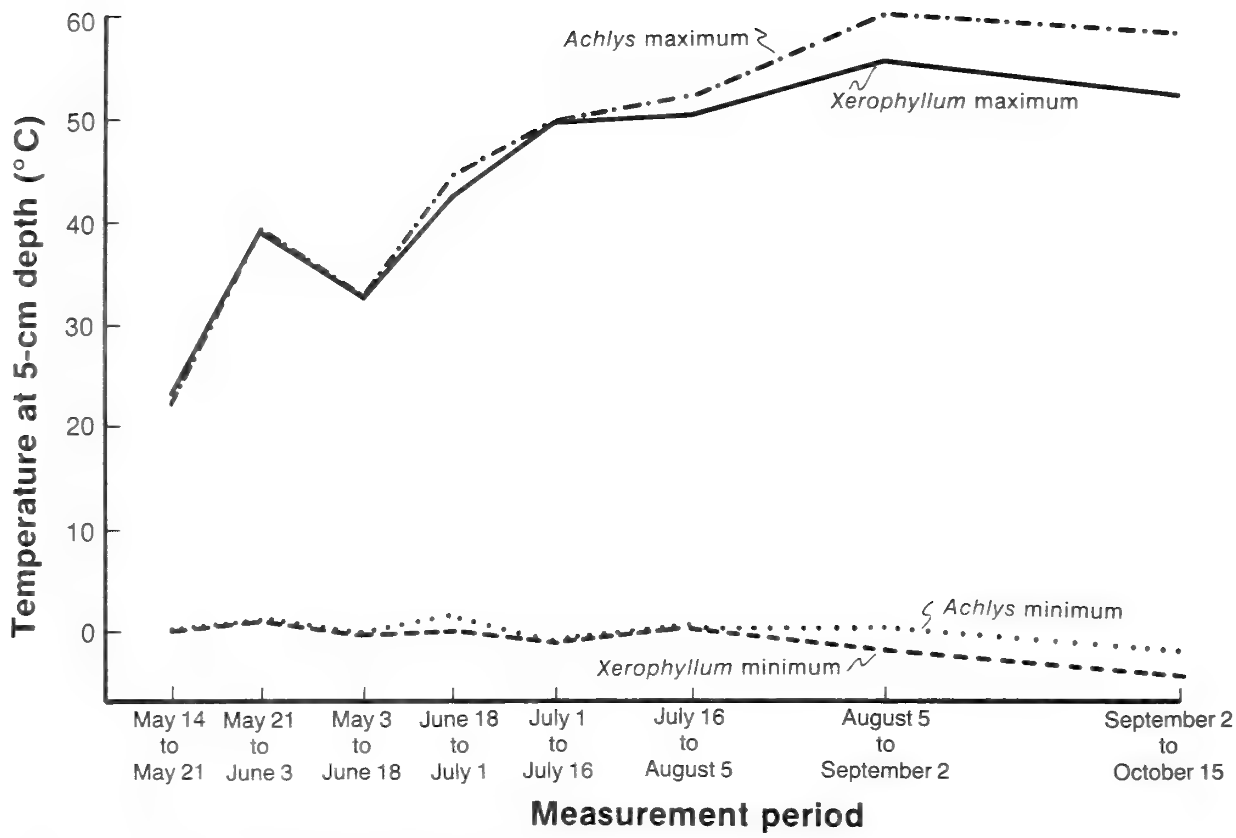

Figure 1.—Seedbed temperatures at the soil surface, summer 1981, by habitat type. Each plotted point is the average of four clearcuts from three randomly distributed, unshaded maximum-minimum thermometers in each clearcut.

(fig. 1), and surface temperatures on several of the most exposed seedbeds exceeded 46 °C during this early period. Average soil surface maximums rose to above 55 °C in August, when the temperatures of several exposed seedbeds exceeded 62 °C. Maximum soil temperatures at a depth of 5 centimeters were less extreme, but the difference between habitat types was evident earlier in the season (fig. 2). Minimum soil surface temperatures were near or below freezing during the entire summer (fig. 1), and I found several seedlings uprooted by frost heaving in October. The minimum soil temperatures at 5 centimeters remained above freezing throughout the summer, but they varied more than the surface minimum temperatures (fig. 2).

Erratum: Germination, survival and early growth of conifer seedlings in two habitat types. Res. Pap. PNW-348. January 1986, p. 10-11: Labels of the y-axes are reversed on figures 1 and 2: figure 1 should be "Temperature at the soil surface (°C)" and figure 2 should be "Temperature at 5-cm depth (°C)."

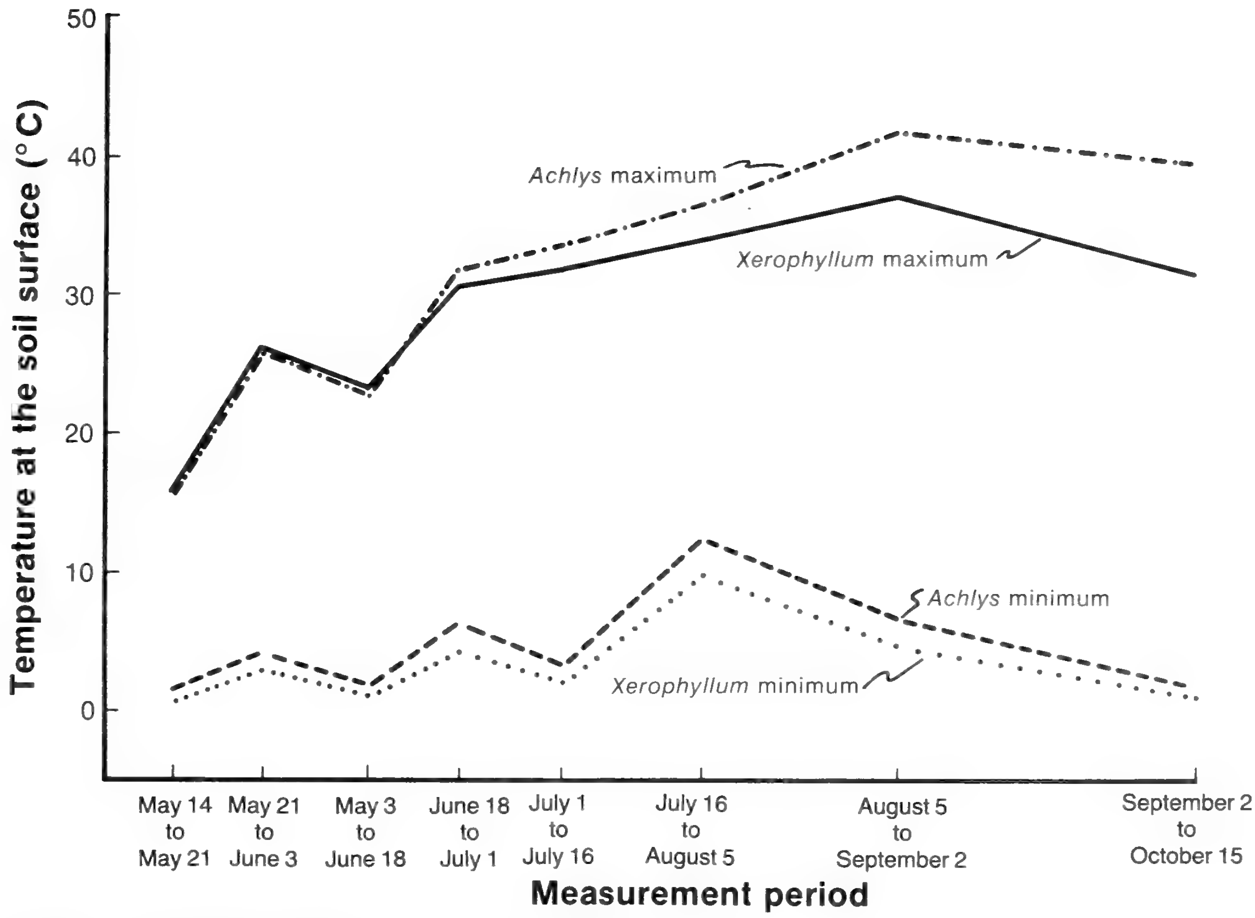

Figure 2.—Seedbed temperatures at the 5-centimeter depth, summer 1981, by habitat type. Each plotted point is the average of four clearcuts, from three randomly distributed, unshaded maximum-minimum soil thermometers with buried sensing probes in each clearcut.

Dense herbaceous vegetation became established on several of the seedbeds, obscuring the conifer seedlings. Seedling survival did not seem to be adversely affected by this vegetative competition. Instead, the shade provided by invading weedy species seemed to benefit seedling survival during the hot, dry month of August 1981. Numbers of invading species and total vegetative cover were higher on the *Achlys* habitat type than on the *Xerophyllum* type.

Animal damage seemed to be more severe on the *Achlys* habitat type than on the *Xerophyllum* type. More gopher mounds were observed on the *Achlys* habitats. Elk completely destroyed one *Achlys* seedbed by trampling the berry baskets and scattering the maximum-minimum thermometers; deer destroyed another.

Dispersed-Seedbed Experiment

Average August temperatures and August precipitation were about normal in 1982 and 1983 (National Oceanic and Atmospheric Administration 1982, 1983). First-year survival at the end of the 1982 growing season was much better on small, dispersed seed spots than it was on the large, consolidated seedbeds. More than 15 percent of the seeds sown under berry baskets survived as 1-year-old seedlings on the seed spots shaded by stumps (table 4). Basket-covered seed spots located on open microsites were less successful, but more than 10 percent of the seeds in that treatment resulted in 1-year-old seedlings. Survival of the seeds without berry-basket protection was much poorer, averaging 1.5 percent on stump-shaded microsites and only 0.8 percent on the open microsites. The first-year, seed-to-seedling ratio was 88:1 for these unprotected seeds.

Variation among clearcuts within habitat types was high. More seedlings survived in the *Xerophyllum* habitats, but the first-year difference in survival between habitat types (10.8 vs 5.8 percent) was not statistically significant. Where mycorrhizal inoculum (humus) was added to the seedbed, 7.8 percent of the seeds survived. Where humus was not added, 8.8 percent survived, but this small difference was not significant. Interactions among habitat type, humus addition, microsites, and predation protection treatments also were not significant 1 year after sowing.

Table 4—Average survival of Douglas-fir seedlings 1 and 2 years after sowing on dispersed seedbeds, by habitat type, humus treatment, microsite, and predation protection

Treatments	1 year after sowing		2 years after sowing		All habitat types	
	Xerophyllum 1/	Achlys 1/	Xerophyllum 1/	Achlys 1/	1 year after sowing 2/	2 years after sowing 3/
	Percent					
Humus added:						
Open microsite--						
Protected	11.2	12.0	7.8	7.5	11.6	7.6
Unprotected	.8	.8	.5	0	.8	.2
Stump-shaded microsite--						
Protected	20.2	14.2	17.5	12.8	17.2	15.2
Unprotected	2.5	1.0	1.8	.2	1.8	1.0
Humus not added:						
Open microsite--						
Protected	19.0	7.2	13.0	4.0	13.1	8.5
Unprotected	1.5	0	.8	0	.8	.4
Stump-shaded microsite--						
Protected	29.0	11.0	25.8	8.0	20.0	16.9
Unprotected	2.5	0	1.0	0	1.2	.5
Average all treatments 4/	10.8	5.8	8.5	4.1	8.3	6.3

1/ Each treatment value is based on 4 clearcut replicates. Each of the 8 treatments in a replicate consisted of 10 widely scattered seed spots with 10 seeds per seed spot.

2/ The microsite and predation protection differences are statistically significant (P<0.01). There are no significant interactions.

3/ The microsite and predation protection differences are significant (P<0.01), and there is a significant (P<0.05) microsite X protection interaction. (Predation protection benefited seedling survival more in the open than on stump-shaded microsites.)

4/ The habitat type differences are not significant (P<0.05).

Two years after sowing, in 1983, the differences in survival between habitat types and between humus treatments remained nonsignificant, but there was a significant interaction between microsite and predation protection (table 4). Protection was more beneficial on open seed spots than it was in the shade of stumps. Stump shade helped, however, in establishing the 2-year-old seedlings; 2-year survival of seeds sown next to stumps (8.4 percent) was twice as great as survival of seeds sown in the open (4.2 percent). The predation protection provided by berry baskets was even more important than stump shade. About 24 times as many 2-year-old seedlings resulted from the original sowing (12.0 vs 0.5 percent) when seeds and young seedlings were protected from predation. The plastic berry baskets deteriorated during the second growing season and did not impede seedling growth (fig. 3).

Figure 3.—Two-year-old Douglas-fir seedlings that have grown through a deteriorating plastic berry basket; September 1983.

Seedling height growth was better next to stumps than in the open, and the seedlings protected from predation grew taller than seedlings without that protection (table 5). Adding forest humus to the seedbeds did not significantly affect seedling heights, and the average 2-year-old heights did not differ significantly between habitat types.

The unprotected seedbeds were most similar to those encountered in nature during natural regeneration. When all of these dispersed, unprotected seedbeds were considered—on all humus treatments—the seed-to-established seedling ratio determined for 2-year-old seedlings on these mineral soil seedbeds was 133:1 on stump-shaded microsites and 333:1 in the open.

Table 5—Average heights of surviving Douglas-fir seedlings 2 years after sowing, by habitat type, humus treatment, microsite, and predation protection

Treatments	Seedlings in Xerophyllum 1/	Seedlings in Achlys 1/	All seedlings 2/
	- - - - - - -	Millimeters	- - - - - - -
Humus added:			
Open microsite--			
Protected	36	54	45
Unprotected	28	--	28
Stump-shaded microsite--			
Protected	49	59	54
Unprotected	28	25	27
Humus not added:			
Open microsite--			
Protected	38	38	38
Unprotected	32	--	32
Stump-shaded microsite--			
Protected	48	53	50
Unprotected	32	--	32
Average all complete treatments 3/	40	46	

-- = absence of surviving seedlings.

1/ Each treatment value is based on the surviving seedlings in 4 clearcut replicates. Each of the 8 treatments in a replicate consisted of 10 widely scattered seed spots with 10 seeds per seed spot.

2/ The microsite and predation protection differences are statistically significant ($P<0.01$). There are no significant interactions.

3/ Complete treatments have seedlings in both habitat types. The habitat type difference is not significant.

Greenhouse Experiment

The soils involved in this study of conifer germination, survival, and early growth were nearly alike. There was some variation in physical and chemical properties among clearcuts, but the two habitat types differed significantly in only one variable. Most of the *Achlys* soils had less extractable Fe than did the *Xerophyllum* soils (table 6). The small habitat type differences in other nutrient elements, texture, color, pH, and cation exchange capacity were not statistically significant.

Table 6—Properties of soils from the *Achlys* and *Xerophyllum* habitat types, by clearcut 1/

Clearcut	Sand 2/	Silt 2/	Clay 2/	pH 3/	C.E.C.	NH_4-N 4/	NO_3-N 4/	P 5/	K 6/	Ca 6/	Mg 6/	Mn 6/	Fe 6/	Munsell color value 7/
	- - - - percent - - - -				meq/100 g	- - - µ/g - - -		p/m	- - - - - - - - mg/100g - - - - - - - -					
Achlys 1	60.3	29.3	10.4	5.15	31.42	19.6	0.020	14.98	7.72	37.18	5.95	1.65	0.192	10 YR 2/1.5
Achlys 2	61.3	33.2	5.5	5.50	25.64	32.2	.043	10.44	7.75	16.95	1.92	1.22	.000	10 YR 2/2.0
Achlys 3	48.4	40.2	11.4	5.30	32.90	30.8	.171	14.98	9.98	26.28	2.58	.80	.000	10 YR 2/2.0
Achlys 4	49.9	38.6	11.5	5.35	37.42	37.8	.115	14.98	5.58	40.60	2.37	.62	.000	10 YR 2/1.0
Mean, all *Achlys*	54.98	35.32	9.70	5.32	31.84	30.1	.087	13.84	7.76	30.25	3.20	1.07	.048	10 YR 2/1.6
Xerophyllum 1	56.5	36.1	7.4	5.05	35.50	61.6	.027	20.88	12.98	16.78	3.13	2.62	.192	10 YR 2/1.5
Xerophyllum 2	54.4	36.2	9.4	5.00	35.78	46.2	.028	17.71	6.82	9.62	1.74	1.32	.288	10 YR 2/1.5
Xerophyllum 3	53.9	34.6	11.5	5.25	39.24	57.4	.054	16.34	9.55	33.92	3.58	1.12	.192	10 YR 2/1.0
Xerophyllum 4	54.7	37.8	7.5	5.40	28.64	29.4	.004	11.35	7.52	13.38	2.20	.75	.192	10 YR 2/2.0
Mean, all *Xerophyllum*	54.88	36.18	8.95	5.10	34.79	48.6	.028	16.57	9.22	18.42	2.66	1.45	0.216	10 YR 2/1.5

1/ Soils were collected from the 0- to 25-centimeter depth at 4 randomly located points on each of the 8 clearcuts. The 4 subsamples from each clearcut were then blended to yield a single sample for that clearcut. The *Xerophyllum* soil has more Fe than the *Achlys* soil, but none of the other parameters differed significantly between habitat types.

2/ Hydrometer method.

3/ Soil-water paste.

4/ Water extractable.

5/ Acid extractable (Bray method).

6/ Extractable (NH_4OA_c at pH 7.0).

7/ Moist soil.

Table 7—Average germination percentages, days to peak germination, mean germination rates with standard deviations, heights, weights, and shoot-to-root ratios of Douglas-fir, noble fir, Pacific silver fir, and western hemlock seedlings grown in a greenhouse on soils from *Abies amabilis/Xerophyllum* and *Abies amabilis/Achlys* habitat types[1/]

Soil type and seedling species	Germination 2/	Peak germination 3/	Mean germination rate and its standard deviation 3/ 4/	Height 2/	Oven-dry shoot weight 5/	Oven-dry root weight 6/	Total oven-dry weight 7/	Shoot-to-root ratio 6/
	percent	days		cm	g	g	g	
Xerophyllum soil:								
Douglas-fir	57.0	103.8	0.0088 ± 0.0020	7.1	1.66	3.07	4.73	0.54
Noble fir	35.0	44.5	.0186 ± .0068	10.8	2.36	4.14	6.50	.55
Pacific silver fir	15.5	67.8	.0120 ± .0045	3.6	.78	1.12	1.90	.73
Western hemlock	61.5	61.0	.0159 ± .0020	7.9	4.69	5.46	10.15	.84
Average, all species	42.2	69.2	.0138 ± .0038	7.3	2.37	3.45	5.82	.64
Achlys soil:								
Douglas-fir	57.5	93.5	.0092 ± .0030	13.4	4.26	5.26	9.50	.76
Noble fir	40.0	38.0	.0200 ± .0090	9.2	2.70	4.90	7.60	.54
Pacific silver fir	19.5	58.5	.0136 ± .0057	5.2	1.86	2.91	4.77	.70
Western hemlock	56.0	60.2	.0158 ± .0025	8.9	2.76	3.67	6.43	.69
Average, all species	43.2	62.6	.0146 ± .0050	9.2	2.89	4.18	7.07	.69

1/ Each species value is the average of 4 replicates. Heights, weights, and shoot-to-root ratios are based on the biggest seedling in each replicate.

2/ Species are significantly different ($P<0.01$), but soil types do not differ significantly, and there are no significant interactions.

3/ Determined by using the method of Campbell and Sorensen (1979). Species and soil types differ significantly ($P<0.01$ and $P<0.05$, respectively), but there are no significant interactions.

4/ Mean germination rate and its standard deviation were used in multivariate analyses of variance. Mean germination time in days equals 1/mean germination rate.

5/ Species differ significantly ($P<0.01$), and there is a significant ($P<0.05$) species-soil type interaction.

6/ Species are significantly different ($P<0.05$).

7/ Species differ significantly ($P<0.05$), and there is a significant ($P<0.05$) species-soil type interaction.

Species differences were significant when germination percentages, days to peak germination, and mean germination rates of the seeds sown on those soils were compared (table 7). Germination percentages for Douglas-fir and western hemlock were higher than those for noble fir and Pacific silver fir, and Douglas-fir germinated more slowly than the other species on soils from both habitat types.

Soil type differences were significant when days to peak germination and mean germination rates were compared among soil types, even though species reacted similarly on the two soil types (there were no significant species × soil type interactions). Seeds of all four conifer species tended to reach their peak germination frequencies faster on *Achlys* soils than on *Xerophyllum* soils, but their germination periods were longer on the *Achlys* soils (figs. 4 through 7). These soil-related differences occurred for both the species that germinated during a brief period (for example, western hemlock, fig. 7) and for those that germinated over a longer period (for example, Douglas-fir, fig. 4). Except for Pacific silver fir (fig. 6), the peak germination frequencies were higher on *Xerophyllum* soils than on *Achlys* soils.

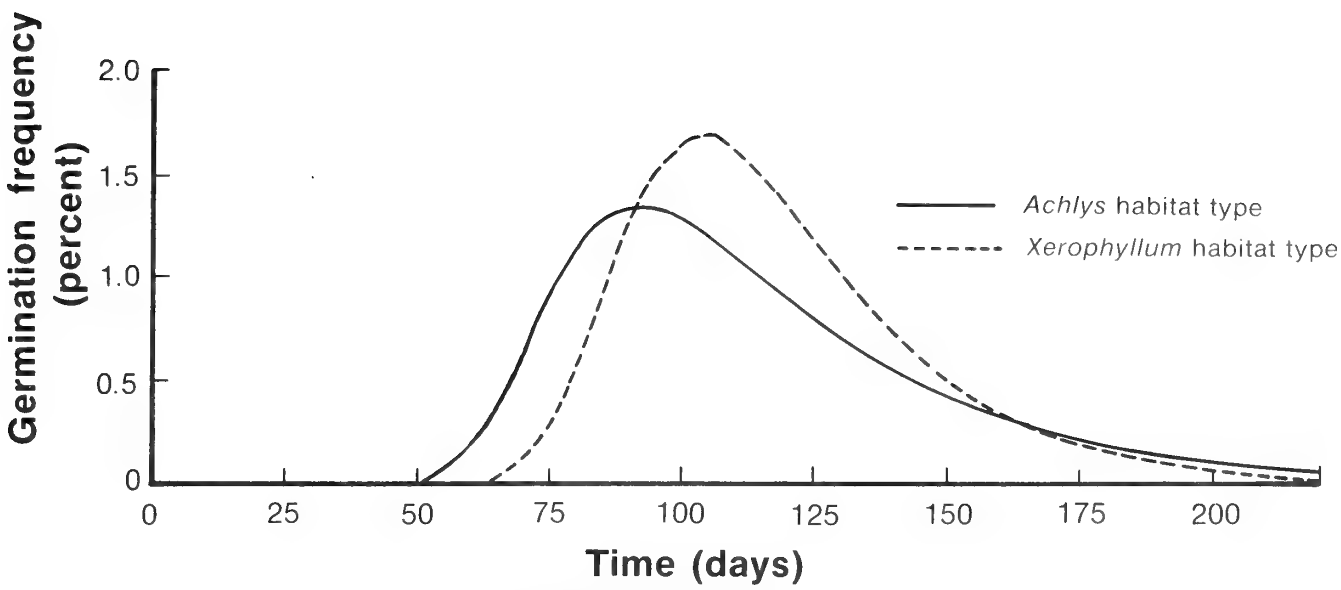

Figure 4.—Germination frequency in an unheated greenhouse of Douglas-fir seeds on soils from *Abies amabilis/Achlys* and *Abies amabilis/Xerophyllum* habitat types.

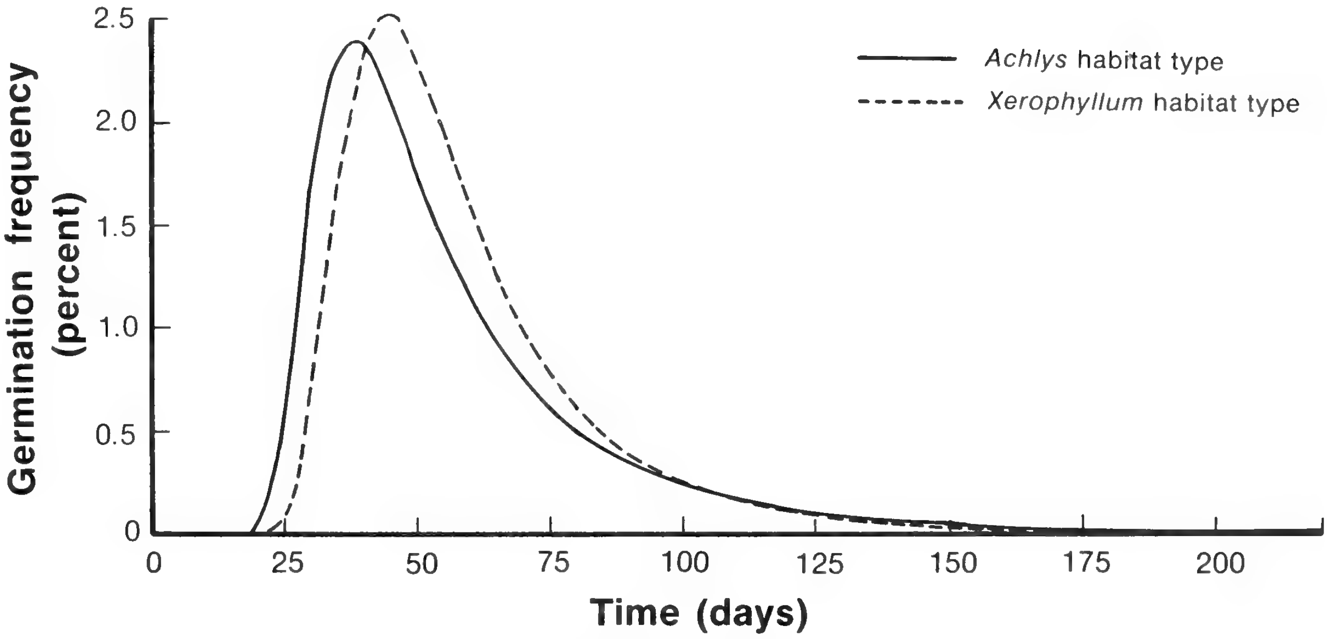

Figure 5.—Germination frequency in an unheated greenhouse of noble fir seeds on soils from *Abies amabilis/Achlys* and *Abies amabilis/Xerophyllum* habitat types.

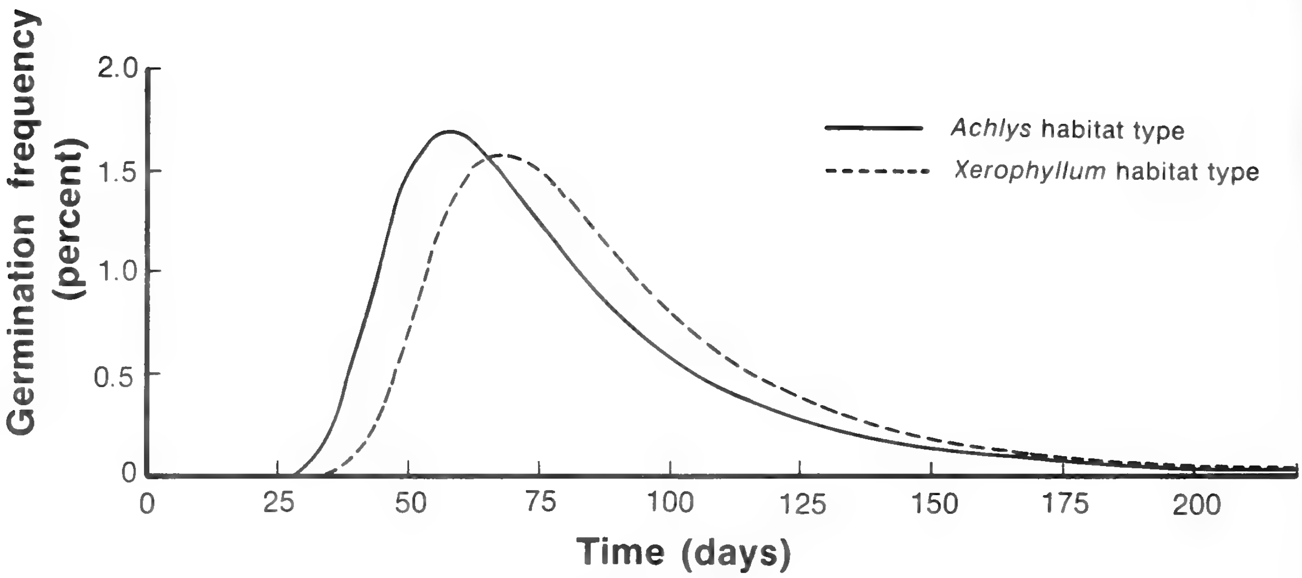

Figure 6.—Germination frequency in an unheated greenhouse of Pacific silver fir seeds on soils from *Abies amabilis/Achlys* and *Abies amabilis/Xerophyllum* habitat types.

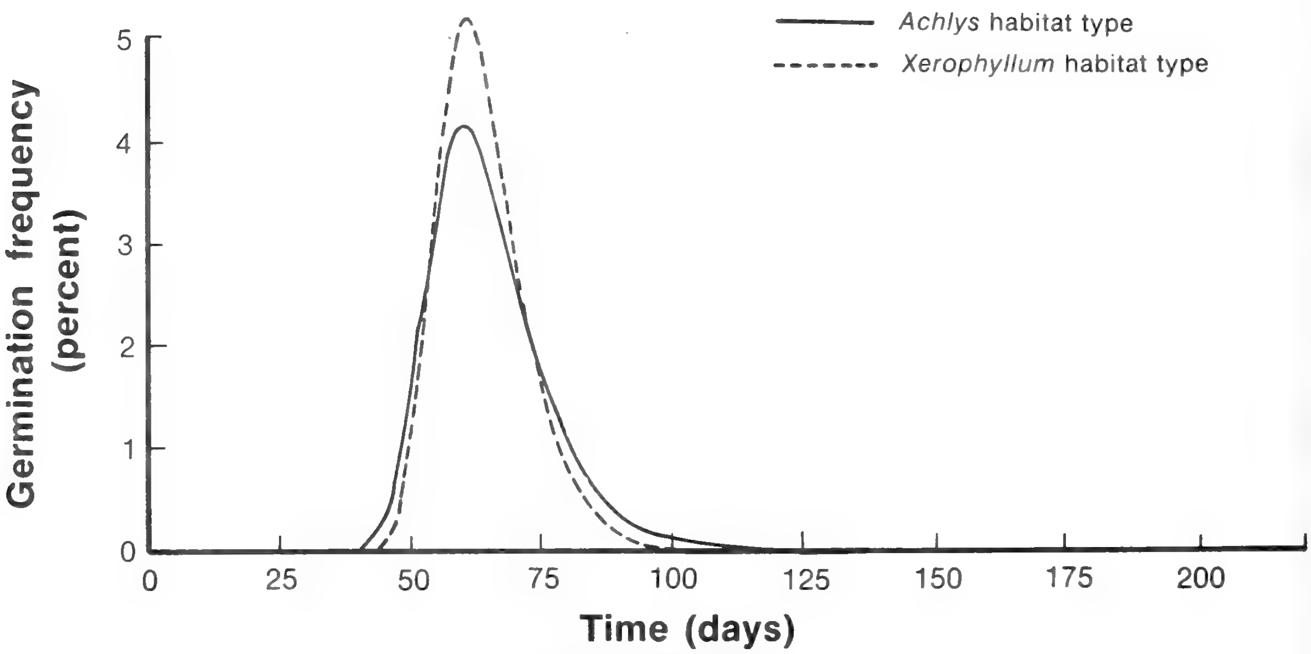

Figure 7.—Germination frequency in an unheated greenhouse of western hemlock seeds on soils from *Abies amabilis/Achlys* and *Abies amabilis/Xerophyllum* habitat types.

The 2-year-old greenhouse seedlings differed in height among species, but those species differences were similar on both soil types, and seedling heights did not differ significantly between soils. Similarly, oven-dry root weights and shoot-to-root ratios differed among species, but the species differences were similar on both soil types, and the soils did not differ with respect to the root weights and shoot-to-root ratios of seedlings grown on them (table 7).

Shoot weights and total seedling weights also differed among species. The species differences were not consistent, however. Although no significant differences in shoot and seedling weights occurred between soil types, the species grew differently on soils from the two habitat types. For example, Douglas-fir shoot and seedling weights were heavier than noble fir shoot and seedling weights on *Achlys* soils, but the reverse was true on *Xerophyllum* soils. Douglas-fir and noble fir seedlings were heaviest on the *Achlys* soils, but western hemlock seedlings were heaviest on the *Xerophyllum* soils.

Discussion and Conclusions

The large size and exposed locations of the consolidated seedbeds made them conspicuous and easy to find. Once found, these 2-meter by 1-meter seedbeds constituted well-spread banquet tables for seed-eating mammals and birds. Most of the seeds were visible, easy to reach, and present in large quantities on a uniform surface. Only seeds under the berry baskets were not easily available at these seedbeds, which seem to have become feeding stations for wildlife. The young seedlings that escaped predation, even those under the berry baskets, were exposed to soil surface temperatures above 55 °C on the consolidated seedbeds. High surface temperatures damage seedlings, and Silen (1960) observed conifer seedling mortality in the field at temperatures of 53 °C to 60 °C. Except for a few seedlings shaded by invading vegetation, none of the consolidated-seedbed seedlings were protected by the irregularities in microtopography and various amounts of partial shade usually found in natural, unmodified seedbeds. Most of the seedlings that escaped mammal and bird predation probably were damaged by high temperatures on the consolidated seedbeds. The observed beneficial effect of competing herbaceous vegetation indicated that moisture stress probably was not serious on those seedbeds.

Whatever its cause, the almost total seed and seedling mortality measured in the consolidated-seedbed experiment should be considered abnormal and not representative of results of either natural regeneration or direct seeding in the *Abies amabilis* forest zone. Too many unforeseen, unnatural seed and seedling hazards were introduced when the consolidated seedbed experiment was designed.

The dispersed-seedbed experiment was designed to avoid the unnatural concentration of seeds and uniform exposure to high seedbed temperatures present in the consolidated seedbeds. Seeds were widely scattered in small seed spots, with different exposures on the stump-shaded and open microsites. A humus treatment was included to see if the absence of mycorrhizal inoculum contained in forest humus might be involved in the variation in survival among clearcuts measured on the consolidated seedbeds.

Introducing humus from adjacent forest stands did not significantly affect the field survival and early growth of Douglas-fir seedlings in the dispersed-seedbed experiment, and variation among clearcuts could not be related to the absence of mycorrhizal inoculum in those clearcuts. Results of the greenhouse experiment suggest that an unmeasured factor like soil microbiology may significantly influence conifer seed germination, however; the simple humus additions tested here do not eliminate humus or mycorrhizae as possible sources of clearcut variation or habitat type differences in conifer germination, survival, and growth within the *Abies amabilis* forest zone.

Habitat type differences in conifer seed germination probably are important. The greenhouse experiment indicates that soils from the *Achlys* habitat type induce earlier, more prolonged germination than do soils from the *Xerophyllum* type when both soils are in the same environment. If this soil-induced difference in germination also occurs in the field, where the *Achlys* habitat type appears to be slightly warmer than the *Xerophyllum* type, germinating seeds in the *Xerophyllum* type would be less likely to experience early and late-season frosts than seedlings in the *Achlys* type—but seedlings in the *Achlys* type might be able to better utilize the abundant soil moisture present after snow melt.

The chemical and physical properties measured in this study do not account for the differences in germination observed on *Achlys* and *Xerophyllum* soils in the greenhouse. The soils were similar with respect to the color, texture, pH, and nutrient variables tested. They occupied randomly assigned positions on the same greenhouse bench and were watered equally. They were never dried, however, and any differences in microbiology present in the field probably were retained in the potted soils. Those unmeasured differences in biological activity may have been responsible for the significant differences in conifer seed germination rates measured on the two soil types in the greenhouse experiment. Other unmeasured soil variables also may have influenced germination rates in the greenhouse. Measurements of conifer seed germination rates on the two soil types in the field were confounded by differences among clearcut and microsite environments.

Microsite environments like those tested in the dispersed-seedbed experiment significantly affect seedling survival and early growth. Stump shade is beneficial, and seeds that fall or are sown on mineral soil near the northeast sides of stumps have a better chance of surviving to become established seedlings than seeds that fall or are sown on soil in the open. They also will produce larger seedlings when located in stump shade if they are protected from animal damage.

Plastic berry baskets used in the two field experiments protected the seedlings from most animal damage. Seedling survival and growth were more affected by the baskets than by any other seedbed variable measured in the dispersed-seedbed experiment. Unfortunately, not all the variables were measured. Many seeds were eaten by small mammals or birds; but many others failed to germinate, were killed by severe environmental conditions, or suffered mechanical damage.

The dispersed-seedbed experiment was not designed to measure the amounts of seed that failed to produce seedlings because of germination failure. Germination of the same Douglas-fir seed lot sown on the same soils in an unheated

greenhouse averaged 57.25 percent, however; a similar germination percent can be assumed in the dispersed-seedbed experiment. If that assumption is made, the amounts of seedling mortality associated with seedbed protection and microsite can be estimated by calculating the differences in survival among treatments listed in the last column of table 4. Bird and small mammal predation caused at least 27 percent mortality. Microsite exposure caused at least another 20 percent. More than half of the observed seedling mortality does not appear to be associated with these two variables. All predation was not prevented by the plastic berry baskets, which were used to measure the amount of bird and small mammal predation; insects penetrated the baskets and large mammals smashed some of them. Similarly, all microsite-related mortality is not represented by the difference between stump-shaded and open-microsite survival, for survival was not assured by putting the seed spots in stump shade. Some stump-shaded environments were quite severe, and sloughing stump bark buried several of the seed spots.

Many other unmeasured variables probably affected the results. The weather and rodent populations that affected my field experiments were assumed to be typical of the area, however, and the same unmeasured variables also affect natural regeneration and direct seeding. The dispersed-seedbed experiment therefore provides a general basis for estimating seedling survival and the seed-to-established seedling ratios to be expected under natural, uncontrolled conditions in the *Abies amabilis* forest zone of the McKenzie River basin. For a Douglas-fir seed lot capable of 100 percent germination, about 75 seeds would be required to establish one 2-year-old seedling on clearcut, mineral soil seedbeds on stump-shaded microsites in the *Abies amabilis/Achlys triphylla* and *Abies amabilis/Xerophyllum tenax* habitat types. About 190 seeds would be required on open microsites. The habitat types do not differ significantly with regard to these seed-to-seedling ratios, for variation among clearcuts within the same habitat type exceeded variation between types.

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English Equivalents

1 millimeter	= 0.03937 inch
1 centimeter	= 0.39370 inch
1 square centimeter	= 0.15500 square inch
1 cubic centimeter	= 0.06102 cubic inch
1 meter	= 3.28083 feet
1 square meter	= 10.76387 square feet
1 hectare	= 2.47104 acres
1 square meter per hectare	= 4.35601 square feet per acre

To obtain Fahrenheit temperature, multiply Celcius temperature by 1.8, then add 32.

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Conifer seeds were sown in clearcut *Abies amabilis/Achlys triphylla* and *Abies amabilis/Vaccinium membranaceum/Xerophyllum tenax* habitat types in the McKenzie River basin in Oregon to determine ratios of seeds to established seedlings. Protection from animal predation and shade from stumps were beneficial, but survival and growth did not differ significantly between habitat types or among humus treatments. Germination in the greenhouse was earlier and more prolonged on soils from the *Achlys* type.

Keywords: Seedling growth, habitat types, seedling survival, germination (seed).

Pacific Northwest Research Station
319 S.W. Pine St.
P.O. Box 3890
Portland, Oregon 97208

U.S. Department of Agriculture
Pacific Northwest Research Station
319 S.W. Pine Street
P.O. Box 3890
Portland, Oregon 97208